

DISTRIBUTION AND COLOR VARIATION OF GYRFALCONS IN RUSSIA

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ABSTRACT.—Gyrfalcon (*Falco rusticolus*) museum specimens in Moscow (73) and St. Petersburg (132) were divided into four color classes (gray, light gray, white gray, and white) and four longitudinal belts representing major physiographic regions of northern Russia. Gray variants predominated in the west and central regions. White birds were most common in extreme eastern Siberia, but were occasionally found even west of the Ural Mountains. Frequencies were as follows: European Russia 4% white, 50% gray (the remainder were intermediates); western Siberia 0% white, 58% gray; central Siberia 15% white, 42% gray; and eastern Siberia 47% white, 33% gray. Remarkably, in the easternmost subregion, white birds predominated even near the southernmost extension.

Because the northernmost portions of the species' range in continental Russia are in central Siberia where white variants were rare, we propose that a better predictor of the white variant is longitude, not latitude. White birds were most frequent at the eastern reaches of both the Palearctic and Nearctic. The best environmental correlates of this distribution pattern may be the southward bending thermal isoclines proceeding eastward toward Greenland or Kamchatka, where both land masses are bathed by cold oceanic currents of Arctic origin. By contrast, the western reaches of both land masses are bathed by warm currents. In these western reaches, Gyrfalcon summer distribution is displaced northward and dark variants predominate.

The breeding range of the Gyrfalcon, determined by mapping the locations of the specimens we examined, differs little from the range proposed in 1951.

Distribución y variación del color en el Gerifalte en Rusia

EXTRACTO.—Especímenes de Gerifalte (*Falco rusticolus*), existentes en museos de Moscú (73) y San Petesburgo (132), fueron separados en cuatro clases de colores (gris, gris claro, blanco grisáceo y blanco) dentro de cada una de las cuatro regiones longitudinales que representan las mayores regiones fisiográficas del norte de Rusia. Las variantes grises predominan en las regiones del oeste y del centro. Las aves blancas son más comunes en el extremo este de Siberia, y hasta son ocasionalmente encontradas al oeste de los Montes Urales. Las frecuencias son las siguientes: Rusia europea 4% blanco, 50% gris (el resto estaba en el intermedio); Siberia occidental 0% blanco, 58% gris; Siberia central 15% blanco, 42% gris; y Siberia oriental 47% blanco, 33% gris. Es de notar que aves blancas predominan aun cerca de la extensión sur de la subregión extremo-oriental.

Las porciones del extremo norte de la región de Rusia continental, donde se halla esta especie, están en Siberia central donde las variantes blancas son raras. Por esto proponemos que un mejor pronosticador de la variante blanca es la longitud y no la latitud. Las aves blancas son más frecuentes en los extremos orientales tanto del Paleártico como del Neártico. El más importante factor de este ambiente, que correlaciona con esta tendencia de distribución, es el isocline termal que se curva hacia el sur y que continúa hacia el este, en dirección de las regiones de Groelandia o Kamchatka que son bañadas por corrientes oceánicas frías de origen ártico. En contraste, el oeste de estas dos regiones es bañado por corrientes cálidas. En estas zonas occidentales, la distribución de verano del *F. rusticoles* se desplaza hacia el norte; y predominan las variantes oscuras.

El área de reproducción de este halcón, basada en los sitios donde fueron colectados los especímenes de museo, no es muy diferente de la propuesta en 1951.

[Traducción de Eudoxio Paredes-Ruiz]

In the four decades since publication of Dementiev's (1951) monograph on the Gyrfalcon (*Falco rusticolus*), little new information has been published in English on this species for the former Soviet Union (comprising nearly 50% of the species' breeding range). Dementiev's (1951) southern limit of breeding is well substantiated by museum specimens, but did not loop south to include the middle Ural Mountains where he (Dementiev 1960) reported that Gyrfalcons bred a century earlier as far south as the Chusovaya, Ufa and Byelaya Rivers (see Fig. 1).

Recent decades have seen a trend in the published literature toward simplifying (i.e., eliminating undulations) and compressing Dementiev's (1951) breeding range without offering supporting data (e.g., Cade 1982, Flint et al. 1984). These changes, if correct, would signal population declines and/or abandonment of formerly occupied range. The boundary we report is little changed from Dementiev's 1951 map, therefore we affirm the accuracy of his map and recommend its continued use until more information is obtained.

Dementiev (1951, 1960) noted the general trend for Gyrfalcons to be lighter in color and larger proceeding eastward across Eurasia. Portenko (1972) also noted that the white variant predominates on the Chukchi Peninsula. We provide frequencies of color variants for the breadth of Russia based on examination of 205 specimens (91 adult and 114 juveniles) in the two primary bird collections in Russia, the University of Moscow Zoological Museum (UMZM) and the Zoological Institute of the Academic Sciences (ZIAS) in St. Petersburg. In discussing color variation, we amplify Vaurie's (1961), Cade's (1982), and Palmer's (1988) observations that Gyrfalcon plumage is infinitely variable along a continuum from the whitest individuals to dark gray or "black" birds. To recognize color phases or, more precisely, color morphs (e.g., white, gray, brown, black) is misleading. It is instructive, however, to report regional trends in the occurrence of light, dark, and intermediate birds.

METHODS

This study is based primarily on examination of the Gyrfalcon skins, specimen tags and catalogues at the UMZM (73 specimens) and the ZIAS (132 specimens). Great effort was expended to translate old Russian script

for dates (from the Julian to Gregorian calendars) and locations (from pre- to post-revolutionary regions). Specimens that lacked sufficient data were excluded from our analysis as were the few birds with spurious data. For example, we excluded ZIAS No. 75403 (which by color and size is a large second-year female Gyrfalcon) because its original label identified it as a male Peregrine Falcon (*F. peregrinus*); its collection date and locale are also better matches for a breeding peregrine.

This study required that we deal with the difficulties presented by the possible taxonomic affinities of the Gyrfalcon, Saker (*F. cherrug*), and Altay (or Altai) Falcon (*F. rusticolus/cherrug altaicus*). Our response was to include only birds that were clearly Gyrfalcons of the non-Altay Falcon type, judging either by collection location and date, or by plumage. This separation was difficult for only a few immatures, those which had the spotted tail pattern thought typical of Sakers. As Cade (1982) indicated, some Sakers also have Gyrfalcon-like barred tails.

We included only one specimen (ZIAS No. 75497) that had previously been treated as an Altay Falcon (cotype of *Gennaia lorenzi*; considered synonymous with *F. r./c. altaicus*, Sushkin 1938, Vaurie 1961). This specimen was a large, gray female Gyrfalcon and lacked the brown dorsal background color that characterizes even the most Gyrfalcon-like of the supposed Altay types. Its location, near the southern end of the Ural Mountains and over 1000 km from the mountains of Central Asia where the Altay Falcon reportedly occurs (Dementiev and Gladkov 1951), and collection date (October or November 1900) are a good match for a migrating Gyrfalcon.

Recognizing that color varies along a continuum (Vaurie 1961), we nonetheless, for comparison purposes, grouped all the specimens into eight age/color classes as follows: white variants (adult and juvenile) were birds with white as a dorsal background color; white gray birds were adults with dorsal dark barring approaching that of gray adults but with very little gray in an otherwise white dorsal background; white brown birds, the corresponding juvenile variant, were pale brown dorsally with light tips and edges and were lightly streaked with brown ventrally on a pale cream background color; light gray birds (and light brown juveniles) had the heavily barred dorsal pattern of normal gray adults (or brown mantle if juveniles) but their dorsal background color, and often the hue of their light and dark bars, was much lighter than the gray variant (or brown variant if juvenile); gray (or brown if juvenile) variants differed from light gray (or light brown) birds in having darker gray (or brown) pigmentation dorsally. Gray adults often had a light gray wash ventrally, especially on tibiae and lower belly, while juveniles had darker ventral streaking and a darker buff wash than other variants. Birds in mixed plumage (molting) provided evidence that the four juvenile classes molt into corresponding adult classes (e.g., white brown juveniles become white gray adults). Examples of adults (and two juveniles) representing most of our light and dark variants are illustrated in Weick's (1980) Plate 39. Juveniles, although often showing a grayish bloom

or even indistinct grayish bars on brown plumage, were never generally gray as Palmer (1988:383, 387) repeatedly states.

Because Gyrfalcons from narrow longitudinal zones probably mix somewhat on the wintering grounds and could thereby confuse our interpretation of regional trends, we analyzed a data subset consisting entirely of falcons collected May through August. Because the number of summer specimens in each longitudinal belt was too small to make all of the comparisons we sought, we increased our sample size by: 1) translating all juvenile plumaged birds into their corresponding adult category, 2) pooling summer and non-summer collections, and 3) pooling 15 longitudinal zones (of 10 degrees each) into four major longitudinal regions that reflect important physiographic regions of Russia (see Fig. 1). These manipulations provided for 70, 60, 33, and 42 birds respectively in the west to east longitudinal regions.

To further minimize the problem of having birds from one longitudinal region in summer collected in a neighboring region in winter, we chose natural physiographic boundaries between regions. The Ural Mountains divide the first two regions, European Russia (30°–60°E) and western Siberia (60°–90°E), and probably serve as an effective barrier to prevent mixing of wintering birds. The latter region, western Siberia, constitutes the lowlands between the Ob and Yenisey Rivers which are unlike the third region, the topographically complex Central Siberian Uplands (90°–150°E). The eastern Siberian region (150°E–169°W) is not well demarcated from the neighboring region to the west. There is, however, a somewhat artificial separation occasioned by the complete lack of specimens for a 10 degree wide boundary (140°–150°E) between the two regions.

We used two methods of contingency table analysis to compare the proportions of each color variant among the four regions. Specimens were assumed to be independent. We know of only one exception to this rule (i.e., two birds were presumed siblings). Because few summer specimens were available, we used Fisher's exact test (Agresti 1990: 59–64) to test the hypothesis that color variants were equally distributed among the regions in summer. For the entire data set, we used log-linear models (Agresti 1990:130–134) to test these same hypotheses. We also used 1 df contrasts for specific tests associated with departures from the hypothesis of equal proportions of color variants among the four regions.

RESULTS AND DISCUSSION

Recent works (e.g., Cade 1982) show summer distribution significantly restricted from that presented by Dementiev (1951). Even publications by Russian authors (Flint and Potapov 1984, Flint et al. 1984), with access to a dozen or so post-1951 Russian language publications on the Gyrfalcon, have also eliminated the irregularities in Dementiev's (1951) line, even though Dementiev's major southward extension in central Siberia was made to accommodate two recently fledged young (ZIAS Nos.

127705 and 127706) collected in July 1918 along the Lower Tunguska River. The summer limit we present (Fig. 1) follows Dementiev's (1951) boundary line and shows the historic southern limit of montane breeding in the central Ural Mountains (Dementiev 1960). Our map also adds one minor southward extension in central Siberia to include a juvenile (ZIAS No. 168211) collected on 16 July 1956 in the upper drainage of the Yana River.

In Figure 1, we also plot a juvenile (ZIAS No. 75428) collected 9 August 1937 in western Siberia near the town of Surgut (on the Ob River) about 450 km south of Dementiev's (1951) line. An adult female collected in June 1904 in Irkutsk Province (central Siberia), most of which is well south of Dementiev's (1951) line, could not be mapped because its collection location information was too general. One or both of these specimens would extend the summer range. Juveniles, however, begin wandering even in July (Cramp et al. 1980) and Dementiev (1951) included neither record, so we omit them also. We suspect, however, that a thorough search of the areas immediately south of our boundary line would, especially in favorable prey years, yield many summer and breeding records.

Our work did not concentrate on winter records. We note, however, that Dementiev's (1951) demarcation of the southern limit of winter distribution of Gyrfalcons extends much further south than illustrated by either Cade (1982) or Cramp et al. (1980). Perhaps the best explanation of this discrepancy is that Cade describes his line as representing the southern limit of the "usual winter migration" range without offering evidence, whereas Dementiev's (1951) line includes all records. Cramp et al. (1980) may have been influenced by authors who reported marked Gyrfalcon declines in western Europe during this century. The only author they cite for Russia, however, presented no information on Gyrfalcon populations (Galushin 1977). There is a sizable corps of field ornithologists and many active field stations in Russia. Until the observational records from these sources are collated, we must rely on the specimen records presented in Dementiev's (1951) monograph.

The distribution of color variants in Russia was discussed briefly by Vaurie (1961). He reported that white birds constitute 50% of the population east of the Lena River (Fig. 1), with white birds found as far west as the Pechora River (just west of the Ural Mountains) and composing 4% of the population

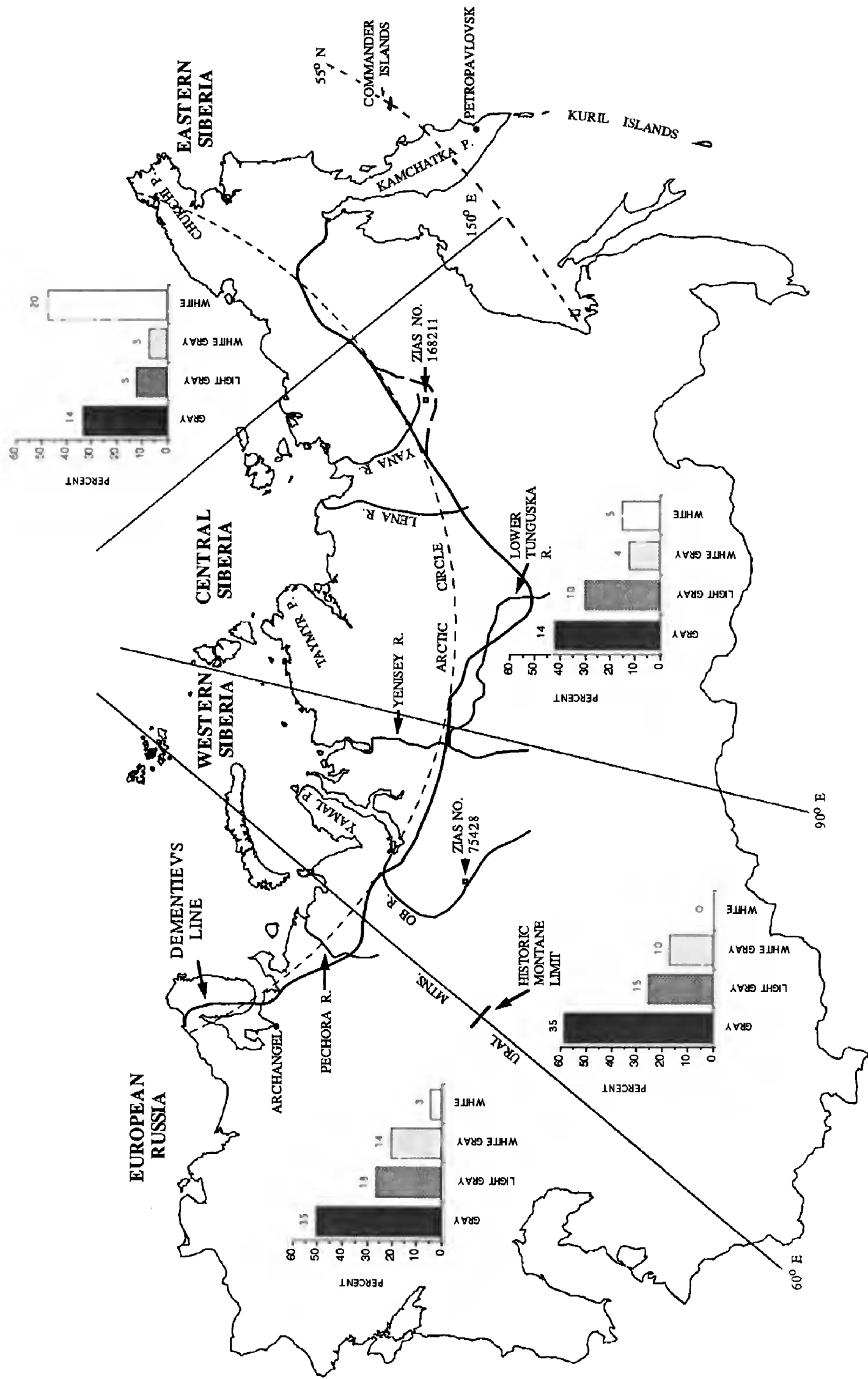


Figure 1. Variation in plumage color and limits of the breeding range of Gyrfalcons in Russia.

Table 1. Number of Gyrfalcon specimens of four color classes collected in four regions of Russian during summer (May–August).

COLOR VARIANT	REGION			
	EURO- PEAN RUSSIA	WESTERN SIBERIA	CENTRAL SIBERIA	EASTERN SIBERIA
Gray	5	4	6	2
Light gray	2	1	4	1
White gray	0	1	0	1
White	1	0	0	4
Total	8	6	10	8

between the Lena and Pechora Rivers. We examined two white adults and one white juvenile from European Russia: the furthest west was an adult (ZIAS 75352) collected in November in the Archangel region. White birds found in winter in European Russia may not represent the continental breeding population, but may be from Spitzbergen or other northern islands. Vaurie (1961) noted that the "black" Gyrfalcon, numerically important only in Labrador in eastern North America, is absent from Eurasia. However, he reported that one bird he examined from Europe was virtually as dark as "black" Gyrfalcons from eastern North America. Further, Dementiev (1960) reported 3 black Gyrfalcons among 99 birds held by a Russian Czar. We did not encounter any dark specimens from European Russia.

It bears mention that Vaurie's (1961) comments and the distributional patterns we report, do not include records for the Altay Falcon (Central Asia) for which many individuals, both juvenile and adult, closely resemble juvenile "black" Gyrfalcons from Labrador. Dementiev (1951:26) had earlier commented on the remarkable "parallel coloration" of the darkest Altay Falcons and the "melanistic variant of the North American Gyrfalcon."

Using the summer specimens alone (Table 1), no significant difference was found ($FI = 11.76$, $P = 0.119$) in the proportions of color classes when all four regions were compared. However, when the specimens from the three westernmost regions, which had no indication of different patterns of color variation ($FI = 5.078$, $P = 0.635$), were combined and compared with those from eastern Siberia, there was a statistically significant difference ($FI = 9.507$, $P = 0.011$). Eastern Siberia had a higher proportion

Table 2. Number (and proportion) of Gyrfalcon specimens of four color classes collected in four regions of Russia.

COLOR VARIANT	REGION			
	EURO- PEAN RUSSIA	WESTERN SIBERIA	CENTRAL SIBERIA	EASTERN SIBERIA
Gray	35 (0.50)	35 (0.58)	14 (0.42)	14 (0.33)
Light gray	18 (0.26)	15 (0.25)	10 (0.30)	5 (0.12)
White gray	14 (0.20)	10 (0.17)	4 (0.12)	3 (0.07)
White	3 (0.04)	0 (0.00)	5 (0.15)	20 (0.47)
Total	70	60	33	42

of white birds and a lower proportion of gray birds than the other regions combined (Table 1).

When we pooled data for the entire year, the most apparent regional trend (Table 2) was the prevalence of white birds in eastern Siberia (47%). Only 33% of the birds in this region were of the gray variant and 67% were lighter than the normal gray type. Proceeding west, the proportion of light gray to white types drops to 57% in central Siberia, then 42% for western Siberia, but rises again to 50% for European Russia even though fully white birds make up only 4% of the latter population. The absence of white specimens for western Siberia is surprising because Pleske (1928) reported white birds for the region, and white nestlings taken from the Yamal Peninsula are now in the propagation project at the Oka State Nature Reserve in Ryazan Province.

The differences in color composition among regions were statistically significant ($\chi^2 = 54.91$, $df = 9$, $P < 0.001$). Based on this test, 1 *df* contrasts yielded the following results. As with the summer specimens, the eastern Siberia region had the highest proportion of white falcons and, conversely, the lowest proportion of the other three variants ($\chi^2 = 41.51$, $P < 0.001$). The sample from central Siberia also had a higher proportion of white birds and a lower proportion of the other variants than either of the two regions to the west ($\chi^2 = 7.21$, $P = 0.007$), but not as large a proportion of white birds as eastern Siberia ($\chi^2 = 9.28$, $P = 0.002$; Table 2).

The data for Russia as a whole seem to contradict Brown and Amadon's (1968:844) generalization that the proportion of white Gyrfalcons increases with increasing latitude. In continental Russia, the northernmost regions occupied by the Gyrfalcon are not

in eastern Siberia where white forms predominate, but around the Taymyr Peninsula in western and central Siberia where white forms are rare. Rather, the strong trend for Russia is for white forms to predominate in the easternmost and perhaps the southernmost extensions of the species' range, the Chukchi and Kamchatka Peninsulas. From Kamchatka, 5 of 17 specimens (29%) were white and 9 of 17 (53%) were of the three lighter variants; for the nearby Commander Islands, 6 of 8 specimens were white. Unfortunately few summer specimens are available from these areas, so little can be said about frequencies of the four variants as breeders, but Stejneger (1885) reports that the white, not the gray, variant is the only known breeding Gyrfalcon on Bering Island, largest of the Commander Islands. Both of the summer adults from Bering Island collected by Stejneger, and now housed at the U.S. National Museum, are white.

Kamchatka and the Commander Islands are also of interest because they extend to and beyond 55°N, the latitude Cade (1982) proposes as the general southern limit of Gyrfalcon breeding. The basis for including all of Kamchatka is perhaps the statement by Dementiev and Gladkov (1951) that the species summers near Petropavlovsk, near the southern tip. Dementiev and Gladkov (1951), however, dispute Yamashina's (1931) claim that the species occasionally breeds further south than Kamchatka, on the middle Kuril Islands.

Kamchatka is mapped within the breeding range by all authors, even Flint et al. (1984), who state, however, that no eyrie has yet been found there. More recently, Lobkov (1986) reported that Gyrfalcons breed regularly on northern Kamchatka. Observations of pairs in summer further south indicate that Gyrfalcons may breed on the east coast as far south as 100–200 km north of Petropavlovsk. Lobkov (1986), however, provides no records for summer pairs on the western slope of Kamchatka, so perhaps the summer range should be adjusted eastward.

The occurrence and even breeding of white birds on the Commander Islands at or beyond Cade's (1982) proposed southern breeding limit is remarkable. Even in North America, white Gyrfalcons, although much more prevalent in northern Greenland and adjacent islands (Salomonsen 1950), are found with fair regularity in Ungava near the southern extremity of the species' North American range (Palmer 1988).

We propose that the primary trend in color variation for Eurasia and probably for the Nearctic (Neoarctic) is for the white variant to become increasingly prevalent proceeding eastward across the two land masses. Prevalence of the white form correlates better with longitude than latitude. A similar trend is also reported for Rough-legged Hawks (*Buteo lagopus*) in the Palearctic (Dementiev and Gladkov 1951:307).

We account for this light in the east and dark in the west phenomenon by examining thermal isoclines and oceanic currents for both land masses. Cleveland (1986) shows that the eastern areas of both regions are colder at comparable latitudes than the central or western regions. This colder east and warmer west pattern is probably best explained by the presence of north flowing, warm oceanic currents along the western reaches of these primary land-masses (the Alaska and Bering Currents for North America, and the Norway Current, the northeast extension of the Gulf Stream, for Scandinavia), and south flowing cold currents bathing the eastern extensions (the east Greenland and Labrador currents for the Nearctic and the Anadyr and Oya currents for Siberia).

Another way to look at the influence of temperature is to compare mean annual temperatures (Cleveland 1986) at the southernmost extensions of Gyrfalcon distribution. Although Labrador and Kamchatka (at the eastern reaches) are far south of Norway and the Alaskan Peninsula (the western reaches), all four areas lie in the same thermal zone (−1° to +4° C mean annual temperature).

If, as suggested by a gross inspection of Gyrfalcon distribution worldwide, ocean current temperatures are of primary importance in determining Gyrfalcon breeding and prevalence of the white variant, then, within broad limits, nesting populations on small islands should reflect this influence even more than populations on large land masses. This means that island-nesting Gyrfalcons should be found further south off the eastern reaches of the two primary land masses and further north off the western reaches. The white form should also be more common on islands than on the mainland at comparable latitudes. The presence of only white breeders on the Commander Islands supports this hypothesis and gives credence to Yamashina's (1931) statement that Gyrfalcons occasionally breed in the middle Kuril Islands (ca. 47°N).

Further, if the ocean temperature theory as stated above is generally correct, local exceptions to this rule should be explicable on the basis of local ocean temperatures. For example, complete absence of white breeders on Iceland, at 65°N and only 300 km from Greenland, seems to violate the general ocean-thermocline rule. On closer inspection, however, we note that Iceland is bathed on all sides by a northward extending tongue of the warm North Atlantic Current (Cleveland 1986) and as a result is better suited for gray birds. Salomonsen (1950:447) reported that for the eastern Nearctic the prevalence of white birds increases with decreasing temperature. A detailed island-by-island comparison of color variant ratios with isotherms for air and water is needed, and may be possible using existing collections worldwide, but is beyond the scope of this paper. We believe that such a treatment will show that midsummer water and/or air temperatures are the best predictors of Gyrfalcon presence and color prevalence worldwide.

To better understand the importance of color polymorphism in the Gyrfalcon, data on summer and winter food habits are needed. These data will be most convincing if dissimilar diets can be demonstrated for white and dark variants in their zones of sympatry.

The ecological significance of various color morphs within a population has been demonstrated for perhaps only one raptor. In the Red-tailed Hawk (*B. jamaicensis*) different color morphs perch, and presumably forage, differently (Preston 1980). Rohwer and Paulson (1987) also discuss the advantages of a predator species having more than one morph within the same population. In addition, the Parasitic Jaeger (*Stercorarius parasiticus*) exhibits a light morph more commonly in the northern parts of its range and a dark morph comprising 70–80% of birds in the southern limits of the species' breeding range in Great Britain (Berry and Davis 1970). These authors report some strong color morph correlates in timing of breeding and prey selection.

The presence of very dark birds in Labrador can perhaps be best explained on the basis that these dark birds are descendants of a population adapted to a warmer or more humid southern climate during a time when a deme of dark falcons was separated by Pleistocene ice from more northerly refugia where white and gray populations persisted (Palmer 1988; see Temple 1972 for a similar explanation of the

evolution of North American races of the Merlin, *F. columbarius*). In recent times, these demes met and to some degree mixed. Today white and black birds occur in both Labrador and Greenland. We propose that the modern day persistence of strong regional trends in color prevalence in the eastern Nearctic is due in part to two factors that impede panmixia. First, the Labrador Sea probably acts as a barrier to gene flow, and second, the light and dark variants probably have a selective advantage where they are most common and are therefore favored.

In summary, extant specimens in the two museums, ZIAS and UMZM, substantiate Dementiev's (1951) summer distribution map. The data for Russia also prompted us to re-evaluate interpretations of environmental correlates of Gyrfalcon distribution and color variation worldwide. It appears that latitude is not the best predictor of Gyrfalcon presence or color. Rather, climate, as reflected by isotherms and as related to the temperature of oceanic currents, better correlates with Gyrfalcon breeding distribution and the prevalence of each color variant. Our conclusion, that climate is more important than latitude, is supported not only by the presence of a higher proportion of white birds at the eastern reaches of both the Nearctic and Palearctic, but also by the extreme southward extensions (south of 55°N) of Gyrfalcon breeding distribution at the eastern reaches in Labrador and Kamchatka and, conversely, northward contractions at the western reaches of both the Palearctic and Nearctic.

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